Effect of Nitrogen on Resistance of Sweet Potato to Sweetpotato Weevil (Coleoptera: Curculionidae) and on Storage Root Chemistry

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ABSTRACT The effects of nitrogen fertilizer on sweet potato, *Ipomoea batatas* (L.) Poir., resistance to the sweetpotato weevil, *Cylas formicarius elegantulus* (Summers), was studied. Adult weevil feeding and oviposition preference, larval survival, and pupal weight were used as measures of sweet potato resistance. Sweet potato resin glycosides and caffeic acid concentrations in the periderm tissue of storage roots also were measured. Sweet potato genotypes (Beauregard, Excel, W-244, W-250, and Sumor) with varying levels of resistance to sweetpotato weevil were grown in the field under three nitrogen regimes (0, 45, and 135 kg N/ha). Harvested storage roots were evaluated in the laboratory for feeding and oviposition activity of sweetpotato weevil female adults under no-choice and choice test conditions. Larval survival rate and pupal weight were determined by rearing the insects individually on storage root sections. Nitrogen level had a significant effect on the number of eggs deposited, but not on the number of feeding punctures. Sweetpotato weevils laid fewer eggs on plants with the highest level of nitrogen. Nitrogen levels did not significantly affect larval survival and pupal weight. Genotype had a significant effect on feeding, oviposition, and larval survival. Beauregard had higher levels of feeding, oviposition, and larval survival compared with the other genotypes. No interaction effects between nitrogen and genotype were significant. Resin glycosides and caffeic acid concentrations were significantly different among genotypes and between years. Nitrogen levels significantly affected the concentrations of caffeic acid in 1997.

KEY WORDS *Cylas formicarius elegantulus*, sweetpotato weevil, nitrogen, plant resistance, resin glycoside, caffeic acid

THE SWEETPOTATO WEEVIL, *Cylas formicarius elegantulus* (Summers), is the most destructive insect pest of sweet potato, *Ipomoea batatas* (L.) Poir., worldwide (Jansson and Raman 1991). It attacks sweet potato in the field and during storage. Eggs are laid in accessible roots or vines, and the larvae develop within the tissue. Larval tunneling induces terpenoid production in the roots, and these terpenoids impart a bitter taste and render even slightly damaged roots unfit for consumption (Uritaini et al. 1975). Because of the concealed nature of the feeding habit, the use of sweetpotato weevil resistant cultivars would be a practical and economical method of control (Collins and Mendoza 1991). Varying levels of resistance have been reported in both field and laboratory evaluations (Mullen et al. 1980a, 1985; Story et al. 1996, 1999a, 1999b, 1999c; Thompson et al. 1999). However, inconsistent performance by selected breeding lines between years and within years at different locations is often encountered, limiting the successful development of commercially useful resistant sweet potato genotypes (Collins et al. 1991).

The expression of host plant resistance to insects can be affected by both biotic and abiotic environmental factors. Identification of these factors would help in the selection and breeding of resistant genotypes. Little research has been done to identify environmental factors that may influence sweet potato resistance to sweetpotato weevil. Nitrogen (N) is a critical element in plant growth and has been recognized as having a role in insect-plant interactions through alterations in nutritional suitability of plant tissue, enzyme activities, and secondary compounds in plants (McNeill and Southwood 1978, Gershenzon 1984). The influence of nitrogenous fertilizer applications on insect behavior, population dynamics, and host plant resistance has been studied for many insect-plant systems (McNeill and Southwood 1978, Mattson 1980, Tingey and Singh 1980, Dowell and Steinberg 1990). The results seem to differ depending on host plant and insect species. Most studies show that insect growth, fecundity, population density, and damage to host plants increase with higher levels of plant N,

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whereas ≈25% of studies indicate a negative correlation or are inconclusive (Scriber 1984a). Some studies have shown that insects tend to prefer a particular level of nitrogen (Archer et al. 1982, Prestidge 1982, Jansson and Smilowitz 1986). These studies suggest that variations in the levels of N in the field may contribute to the variability of insect resistance in plants. In this study, we investigated the effects of nitrogenous fertilizer applied during the growing season on sweetpotato weevil feeding, ovipositional activities (no-choice tests), and preference among different genotypes (choice tests) under laboratory conditions. Larval survival rate and growth (represented by pupal weight) on storage roots also were evaluated. In addition, the concentrations of sweet potato resin glycosides and caffeic acid in the periderm tissue of storage roots were measured because these two compounds are believed to be related to pest resistance in sweet potato (Peterson and Harrison 1992, Peterson et al. 1998, Jackson and Peterson 2000).

Materials and Methods

Field experiments were conducted at the Burden Research Plantation, LSU Agricultural Center, Baton Rouge, LA. In 1997, two genotypes, Beauregard and Excel, and two breeding lines, W-250 and W-244 (obtained from the sweet potato breeding program of Janice R. Bohac, U.S. Vegetable Laboratory, USDA-ARS, 2875 Savannah Highway, Charleston, SC) were used. Beauregard is susceptible to sweetpotato weevil, while the other lines have shown a moderate level of resistance (Story et al. 1999a, 1999b, 1999c). In 1998, the genotype Sumor was used in place of W-250 because the resistance of W-250 was low in 1997 tests. The treatments were 3 × 4 factorial combinations of three N levels (0, 45, and 135 kg N/ha) by four genotypes (lines) arranged in a randomized complete block design with six blocks. Each treatment consisted of three seven-plant rows using a 0.3-m spacing within rows and 1.0-m spacing between rows. Sweet potato slips were transplanted on 17 July 1997 and 23 June 1998. Before transplanting, commercial fertilizer (N-P-K: 8-24-24) was applied at the rate of 45 kg N/ha for both 45 and 135 kg N/ha plots. The 0 kg N/ha plots received the same amount of non-nitrogen fertilizer (0-24-24). Two additional applications of ammonium nitrate (34% N) at the rate of 45 kg N/ha were made for the 135 kg N/ha plots at 40 and 75 d after transplanting. Storage roots from the central row were harvested at 110 d after transplanting, cured (30°C, 90% RH for 7 d), and stored at 15 ± 2°C, until used in insect bioassays and chemical analysis.

Two leaf samples (blades only) were taken in 1997 from four of the six blocks at 60 and 95 d after transplanting. The samples were rinsed with deionized water, dried at 70°C, and ground with a mortar and pestle to pass a 20-mesh screen. Total N was determined using a FP-428 Nitrogen Analyzer (LECO, St. Joseph, MI).

Insect Rearing. A sweetpotato weevil colony was established from a field collected population (≈500 adult insects) and maintained in the laboratory on storage roots of Beauregard in plastic containers (5.6 liter) with screen covers at 28 ± 2°C and 85 ± 10% RH. In preparing experimental insects, five fresh storage roots (US #1) were exposed to ≈1000 unsexed adults for 5 d, and then removed and kept under the conditions described above. Emerging adults were collected weekly and held with fresh storage roots. Female adults 3–4 wk old were used in the bioassays to ensure adequate egg-laying capability (Wilson et al. 1988).

Feeding and Oviposition Bioassay. The assay technique was an adaptation of one previously described by Mullen et al. (1980b) and has been used in several sweetpotato weevil feeding and oviposition studies (Nottingham et al. 1987, Wilson et al. 1988). It consisted of a 24-well tissue culture plate (12.5 by 8.5 by 2.0 cm; Falcon model 3047, Becton Dickenson, Lincoln Park, NJ) placed in a rectangular clear plastic container (17 by 12 by 6 cm; Tri-State Plastic, Latonia, KY). Cores were cut from selected roots with a cork borer (1.6 cm diameter) and inserted into the wells so that only the surface of the root periderm was exposed. The diameters of the cores were the same diameter as the wells, providing for a tight fit. Female adults were kept without food for 3 h before being introduced into the arena at the rate of two weevils per root core. A moist cotton ball was placed in the container to maintain 90–100% RH and prevent desiccation of the root cores. The number of feeding punctures on each core was recorded after 24 h, and the number of eggs was counted after 48 h. Bioassays were conducted at 28 ± 2°C and 85 ± 10% RH under total darkness to eliminate light as a variable. Roots from all 12 treatments and six blocks were tested in the bioassay in 1997. In 1998, roots from one block were discarded because of the presence of weevils, leaving five blocks for testing. In no-choice tests, a single root core from one treatment was presented to the weevils. In choice tests, 12 root cores were placed in the arena, each cut from one randomly selected root from each treatment within a given block. For each block, the tests were repeated four to eight times depending upon the availability of roots.

Larval Survival and Development Bioassay. Sweetpotato weevils were reared individually on storage roots in petri dishes by transferring a single egg into a root section (≈1.5 by 1.5 by 1.5 cm) with a cavity (1–2 mm deep, cut with a No. 1 cork borer) for its reception. Eggs were obtained by exposing Beauregard storage roots to a large number of females for 24 h. A needle nosed forceps was used to gently transfer the eggs. At 12 d after the eggs were deposited, the root sections were examined to determine if the eggs had hatched. Nonviable eggs or rotten root sections were discarded. At 25 d after oviposition, root sections were dissected to locate pupae. Larval survival and pupal weights were recorded. Roots from all 12 treatments were tested using a completely randomized experimental design, with sample sizes ranging from 19 to 32 observations per treatment. The variable sample size was due to egg mortality. Bioassays were conducted

Table 1. Leaf nitrogen concentration (% N) of four sweet potato genotypes grown under three nitrogen regimes in 1997

N regime	Beauregard	Excel	W-244	W-250	Means[a]
0 kg/ha N	4.04 ± 0.12	3.26 ± 0.46	3.53 ± 0.25	3.31 ± 0.52	3.54 ± 0.18a
45 kg/ha N	4.08 ± 0.12	3.36 ± 0.22	3.62 ± 0.35	3.40 ± 0.31	3.62 ± 0.17a
135 kg/ha N	4.56 ± 0.11	4.14 ± 0.29	4.17 ± 0.14	4.24 ± 0.38	4.28 ± 0.13b
Means[b]	4.23 ± 0.17a	3.57 ± 0.28a	3.77 ± 0.20a	3.65 ± 0.30a	

Means (±SEM, n = 4) of leaf samples taken at 60 and 95 d after treatment.
[a] Main effects of N regime; means followed by the same letter within column are not significantly different ($P < 0.05$, Tukey test).
[b] Main effects of cultivar; means followed by the same letter within row are not significantly different ($P < 0.05$, Tukey test).
ANOVA results: Nitrogen: $F = 7.25$; df = 2, 36; $P < 0.01$. Cultivar: $F = 2.76$; df = 3, 36; $P = 0.06$. Interaction: $F = 0.16$; df = 6, 36; $P = 0.99$.

under conditions of 28 ± 2°C and 85 ± 10% RH and total darkness.

Chemical Analysis. Sweet potato roots were carefully washed under flowing water and dried. A randomized complete block experimental design was used, with 3–5 roots from each treatment within each block used to produce one sample for chemical analysis. Periderm tissue was gently scraped off the roots with a scalpel. Only healthy and undamaged roots were used to prevent contamination from stress-induced metabolites. The periderm was dried at 50°C, and ground to a fine powder under liquid nitrogen using a mortar and pestle. Subsequently the powder was redried and stored in vials under nitrogen in a freezer until analysis. Samples (200 mg) were placed in Teflon-lined, screw-capped test tubes, and 2.0 ml of methanol containing 0.08 mg of chrysin (recrystallized from amyl alcohol) was added. The test tubes were ultrasonicated for 20 min while the surrounding water was cooled with ice. The tubes were centrifuged and the supernatant filtered through Nylon-66 membrane filters (0.20 μm; Pierce Chemical, Rockville, IL) into auto injector vials for analysis.

Resin glycoside and caffeic acid concentrations were analyzed by reversed phase HPLC using 20 μl of the solution. For resin glycoside, a H_2O/MeOH linear gradient from 60 to 100% MeOH in 15 min was used and held at 100% MeOH for 25 min.; flow rate was 1 ml min^{-1} and detection was at 230-nm. A second injection was made for caffeic acid analysis. A H_2O/MeOH linear gradient from 10 to 100% MeOH in 35 min was used and held at 100% MeOH for 25 min.; flow rate was 1 ml min^{-1} and detection was at 340-nm. Each solvent contained 0.1% H_3PO_4. The column was a Beckman Ultrasphere C_{18}, 5 μm (4.6 by 250 mm; Beckman and Coulter, Fullerton, CA). Purified substances were used as external standards to determine response factor versus chrysin for quantification. Reference glycoside material was purified using Sephadex column chromatography followed by semipreparative HPLC as described previously (Peterson et al. 1998). Reference caffeic acid was purchased from Aldrich (Milwaukee, WI).

Data Analysis. Data were analyzed using the general linear model procedure PROC GLM with a factorial treatment structure followed by the Tukey test for mean comparisons (SAS Institute 1990). Percentage larval survival data were converted by square-root transformation to obtain a homogenous variance. Year effect was analyzed by pooling the two years of data together with a nested treatment structure model. The significance level was $\alpha = 0.05$.

Results

Concentration of Total Leaf N. N regime had a significant effect on the concentration of nitrogen in the leaves of plants, with the higher N regime having higher levels of leaf nitrogen (Table 1). The concentration of nitrogen in the leaves did not differ among the four genotypes. The N and genotype interaction was not significant, suggesting that genotypes responded to N regime in a similar manner.

Feeding and Oviposition. The main effects of N regime and genotype were examined since no significant interaction effects were found (Table 2). N regime did not have a significant effect on the number of feeding punctures in 1997 and 1998. N regime had a significant effect on the number of eggs deposited in 1997 (choice tests only) and in 1998 (both choice and no-choice tests). Fewer eggs were laid under the 135-kg N/ha regime than under the 45-kg N/ha regime.

Genotype had a significant effect on the number of feeding punctures in 1997 and 1998 under both choice and no-choice conditions (Table 2). More feeding punctures were present on the susceptible genotype Beauregard than the four resistant genotypes. These differences were significant in most genotypes in both testing situations and in both years. Genotype had a significant effect on the number of eggs deposited in 1997 (choice tests only) and 1998 (both choice and no-choice tests). Beauregard received significantly more eggs than the resistant genotypes in 1998 (both choice and no-choice tests) but not in 1997 (with a single exception of W-244 in the choice test). Among the resistant genotypes, there were not any obvious trends in the number of eggs deposited.

The year effect was significant in the number of feeding punctures and eggs in no-choice tests (feeding punctures: $F = 40.65$; df = 1, 103; $P < 0.01$. eggs: $F = 6.25$; df = 1, 103; $P = 0.01$), but not significant in choice tests (feeding punctures: $F = 2.54$; df = 1, 103; $P = 0.1139$. eggs: $F = 0.02$; df = 1, 103; $P = 0.9012$).

Larval Survival and Pupal Weight. The main effects of N regime and genotype were examined since no significant interaction effects were found (Table 3). N regime did not have a significant effect on larval survival and pupal weight in 1997 or 1998. All three N regimes had similar larval survival and pupal weight. Genotype had a significant effect on larval survival in

Table 2. Main effects of nitrogen and genotype on sweetpotato weevil adult feeding and oviposition under no-choice and choice test conditions in 1997 and 1998

Main effects	1997				1998			
	No-choice test		Choice test		No-choice test		Choice test	
	No. feeding punctures[a]	No. eggs[b]	No. feeding punctures[c]	No. eggs[d]	No. feeding punctures[e]	No. eggs[f]	No. feeding punctures[g]	No. eggs[h]
0 kg/ha N	22.3 ± 1.08a	10.5 ± 0.52a	27.7 ± 2.34a	10.2 ± 0.61ab	30.0 ± 2.45a	9.7 ± 0.56b	31.2 ± 2.82a	9.9 ± 0.66ab
45 kg/ha N	23.7 ± 1.19a	10.7 ± 0.48a	28.8 ± 2.46a	11.0 ± 0.56a	31.2 ± 2.06a	11.1 ± 0.47a	32.8 ± 3.19a	10.8 ± 0.51a
135 kg/ha N	23.0 ± 1.28a	10.6 ± 0.42a	27.5 ± 2.14a	8.7 ± 0.59b	28.3 ± 2.49a	8.6 ± 0.61b	29.7 ± 2.33a	9.0 ± 0.71b
Beauregard	26.4 ± 1.34a	10.6 ± 0.48a	35.7 ± 2.32a	10.6 ± 0.42a	40.1 ± 1.64a	12.8 ± 0.55a	43.6 ± 1.90a	12.9 ± 0.60a
Excel	22.7 ± 1.19b	11.2 ± 0.50a	26.5 ± 1.61bc	10.7 ± 0.39a	29.9 ± 2.72b	9.3 ± 0.45b	37.3 ± 2.38a	9.3 ± 0.45b
W-244	19.9 ± 1.13c	10.1 ± 0.54a	20.7 ± 2.36c	8.2 ± 0.75b	28.0 ± 2.31b	8.2 ± 0.62b	27.0 ± 1.95b	7.6 ± 0.71c
W-250/Sumor[i]	22.9 ± 1.39b	10.6 ± 0.64a	29.2 ± 2.96ab	10.3 ± 0.97a	21.4 ± 1.35b	8.9 ± 0.40b	16.9 ± 0.69c	9.7 ± 0.43b

Means ± SEM within a column and main effect followed by the same letter are not significantly different ($P < 0.05$, Tukey test).
[a] Nitrogen: $F = 1.28$; df = 2, 55; $P = 0.29$. Cultivar: $F = 13.92$; df = 3, 55; $P < 0.01$. Interaction: $F = 0.84$; df = 6, 55; $P = 0.54$.
[b] Nitrogen: $F = 0.14$; df = 2, 55; $P = 0.87$. Cultivar: $F = 2.09$; df = 3, 55; $P = 0.11$. Interaction: $F = 2.02$; df = 6, 55; $P = 0.08$.
[c] Nitrogen: $F = 0.18$; df = 2, 55; $P = 0.84$. Cultivar: $F = 9.91$; df = 3, 55; $P < 0.01$. Interaction: $F = 0.95$; df = 6, 55; $P = 0.47$.
[d] Nitrogen: $F = 6.92$; df = 2, 55; $P < 0.01$. Cultivar: $F = 5.45$; df = 3, 55; $P < 0.01$. Interaction: $F = 1.69$; df = 6, 55; $P = 0.14$.
[e] Nitrogen: $F = 0.87$; df = 2, 44; $P = 0.42$. Cultivar: $F = 18.00$; df = 3, 44; $P < 0.01$. Interaction: $F = 0.33$; df = 6, 44; $P = 0.92$.
[f] Nitrogen: $F = 15.87$; df = 2, 44; $P < 0.01$. Cultivar: $F = 30.27$; df = 3, 44; $P < 0.01$. Interaction: $F = 0.93$; df = 6, 44; $P = 0.48$.
[g] Nitrogen: $F = 0.88$; df = 2, 44; $P = 0.42$. Cultivar: $F = 36.45$; df = 3, 44; $P < 0.01$. Interaction: $F = 0.30$; df = 6, 44; $P = 0.94$.
[h] Nitrogen: $F = 5.72$; df = 2, 44; $P < 0.01$. Cultivar: $F = 26.10$; df = 3, 44; $P < 0.01$. Interaction: $F = 0.37$; df = 6, 44; $P = 0.89$.
[i] Data are from W-250 in 1997 and from Sumor in 1998.

both years, but not on pupal weight. In 1997, sweetpotato weevil reared on Beauregard had a significantly higher rate of survival than individuals reared on the resistant genotypes. W-244 had the lowest survival rate (81.7%) of all genotypes. In 1998, weevils reared on Beauregard again had a significantly higher rate of survival than individuals reared on the resistant genotypes, whereas no difference was found among the three resistant genotypes. Weevils had similar pupal weight on all genotypes. The year effect was not significant for larval survival ($F = 2.91$; df = 1, 23; $P = 0.10$) and pupal weight ($F = 0.26$, df = 1, 23; $P = 0.62$).

Resin Glycosides and Caffeic Acid Concentrations. N regime did not have a significant effect on the concentration of resin glycosides in both years (Table 4). N regime had a significant effect on caffeic acid concentration in 1997 (where higher N levels were associated with a higher concentration of caffeic acid) but no effect was detected in 1998 (Table 4). Genotype had a significant effect on both compounds in 1997 and 1998. Resin glycosides concentrations were significantly different among all genotypes in 1997, where Excel had the highest concentration followed by W-244, Beauregard, and W-250. W-250 had the highest caffeic acid concentration followed by Excel, Beauregard, and W-244. In 1998, Excel again had a higher concentration of resin glycosides than the other three genotypes. Sumor had a higher concentration of caffeic acid compared with the other three genotypes (Table 4). The year effect was significant for both chemicals (resin glycosides: $F = 28.05$; df = 1, 109; $P < 0.01$. caffeic acid: $F = 39.36$; df = 1, 109; $P < 0.01$). The concentration of resin glycosides was higher in 1997 than in 1998. The concentration of caffeic acid was lower in 1997 than 1998.

Discussion

Our study indicates that the tested N regimes did not appreciably influence the feeding behavior of the

Table 3. The main effects of nitrogen and genotype on sweetpotato weevil larval survival and pupal weight in 1997 and 1998

Main effect	1997		1998	
	Larval survival[a] (%)	Pupal weight[b] (mg)	Larval survival[c] (%)	Pupal weight[d] (mg)
0 kg/ha N	92.0 ± 2.65a	7.44 ± 0.11a	91.1 ± 1.57a	7.51 ± 0.18a
45 kg/ha N	88.5 ± 2.98a	7.67 ± 0.15a	92.1 ± 1.90a	7.93 ± 0.09a
135 kg/ha N	89.8 ± 2.43a	7.98 ± 0.17a	92.4 ± 2.14a	7.48 ± 0.17a
Beauregard	98.9 ± 0.70a	7.49 ± 0.22a	98.1 ± 1.31a	7.24 ± 0.28a
Excel	89.5 ± 2.91b	7.77 ± 0.17a	89.8 ± 1.43b	7.69 ± 0.15a
W-244	81.7 ± 1.34c	7.96 ± 0.21a	89.9 ± 1.86b	7.85 ± 0.11a
W-250/Sumor[e]	90.2 ± 1.41b	7.56 ± 0.13a	89.7 ± 1.65b	7.87 ± 0.09a

Means ± SEM within a column and main effect followed by the same letter are not significantly different ($P < 0.05$, Tukey test). Percentage larval survival data were transformed to square-root before analysis. Means of untransformed data are presented.
[a] Nitrogen: $F = 1.99$; df = 2, 11; $P = 0.18$. Cultivar: $F = 23.76$; df = 3, 11; $P < 0.01$. Interaction: $F = 2.47$; df = 6, 11; $P = 0.09$.
[b] Nitrogen: $F = 3.75$; df = 2, 11; $P = 0.06$. Cultivar: $F = 1.66$; df = 3, 11; $P = 0.23$. Interaction: $F = 1.11$; df = 6, 11; $P = 0.41$.
[c] Nitrogen: $F = 0.20$; df = 2, 11; $P = 0.82$. Cultivar: $F = 5.71$; df = 3, 11; $P = 0.01$. Interaction: $F = 0.86$; df = 6, 11; $P = 0.55$.
[d] Nitrogen: $F = 3.44$; df = 2, 11; $P = 0.07$. Cultivar: $F = 3.09$; df = 3, 11; $P = 0.07$. Interaction: $F = 0.27$; df = 6, 11; $P = 0.94$.
[e] Data are from W-250 in 1997 and from Sumor in 1998.

Table 4. The main effects of nitrogen and genotype on resin glycoside and caffeic acid concentrations in the periderm tissue of sweet potato storage roots in 1997 and 1998

Main effect	1997		1998	
	Resin glycoside[a] (% DW)	Caffeic acid[b] (% DW)	Resin glycoside[c] (% DW)	Caffeic acid[d] (% DW)
0 kg/ha N	2.47 ± 0.316a	0.32 ± 0.018b	1.67 ± 0.266a	0.41 ± 0.014a
45 kg/ha N	2.41 ± 0.320a	0.34 ± 0.018ab	1.84 ± 0.158a	0.41 ± 0.021a
135 kg/ha N	2.28 ± 0.309a	0.37 ± 0.018a	1.66 ± 0.184a	0.44 ± 0.014a
Beauregard	1.97 ± 0.720c	0.33 ± 0.054b	1.45 ± 0.157b	0.42 ± 0.023b
Excel	4.33 ± 0.821a	0.37 ± 0.066ab	2.68 ± 0.286a	0.40 ± 0.015b
W-244	2.71 ± 0.742b	0.27 ± 0.106c	1.35 ± 0.198b	0.39 ± 0.016b
W-250/Sumor[e]	0.54 ± 0.261d	0.40 ± 0.068a	1.36 ± 0.124b	0.48 ± 0.015a

Means ± SEM within a column and main effect followed by the same letter are not significantly different ($P < 0.05$, Tukey test).
[a] Nitrogen: $F = 0.58$; df = 2, 55; $P = 0.57$. Cultivar: $F = 121.77$; df = 3, 55; $P < 0.01$. Interaction: $F = 0.98$; df = 6, 55; $P = 0.44$.
[b] Nitrogen: $F = 4.34$; df = 2, 55; $P = 0.02$. Cultivar: $F = 13.78$; df = 3, 55; $P < 0.01$. Interaction: $F = 0.88$; df = 6, 55; $P = 0.52$.
[c] Nitrogen: $F = 0.27$; df = 2, 49; $P = 0.77$. Cultivar: $F = 14.55$; df = 3, 49; $P < 0.01$. Interaction: $F = 0.64$; df = 6, 49; $P = 0.70$.
[d] Nitrogen: $F = 1.84$; df = 2, 49; $P = 0.17$. Cultivar: $F = 7.55$; df = 3, 49; $P < 0.01$. Interaction: $F = 2.04$; df = 6, 49; $P = 0.08$.
[e] Data are from W-250 in 1997 and from Sumor in 1998.

sweetpotato weevil. Weevils showed a slight non-preference for the highest level of N for oviposition. This trend was present regardless of genotype. Weevils placed on resistant genotypes had lower feeding and oviposition rates and lower larval survival, suggesting both antixenosis and antibiosis may be mechanisms involved in this resistance. However, N seems to modify only the antixenosis component, since N did not significantly affect larval survival or pupal weight.

Sweetpotato weevil eggs are deposited in cavities produced from feeding. Feeding and oviposition appear to be closely related (Ratnayake 1995). However, the insect feeds on all parts of the host plant but only deposits eggs on storage roots and basal parts of the stem (Reinhard 1923). Such behavior suggests that different factors within the plant mediate the feeding and oviposition activities. Wilson et al. (1989) indicated that feeding and/or egg cavity formation and oviposition might be stimulated by different cues. Our results also suggest that sweetpotato weevil feeding and oviposition behaviors may be mediated by different host plant cues since N affected the number of eggs deposited but not the number of feeding punctures.

Nitrogen availability can alter the production of secondary plant chemicals and thereby influence the activity of herbivores (Scriber 1984b, Haukioja et al. 1985). Boehmeryl acetate is a secondary plant compound, identified as a sweetpotato weevil ovipositional stimulant in sweet potato root periderm (Son 1989). The amount of boehmeryl acetate has been correlated with oviposition (Wilson et al. 1989). Marti et al. (1993) indicated that the N and K concentrations in sweet potato leaves had effects on storage root surface chemistry. Therefore, the effect of N on oviposition may be due to an alteration in the production of ovipositional stimulants. The genus *Ipomoea* contains numerous secondary compounds that are produced either constitutively or upon induction by external agents (Kays 1992). Sweet potato resin glycosides and caffeic acid in root periderm tissue are two compounds that have antibiotic activities to insects (Peterson and Harrison 1992). Jackson and Peterson (2000) reported sublethal effects of the resin glycosides on *Plutella xylostella* L. Caffeic acid showed adverse effects on a generalist herbivore, *Helicoverpa zea* (Boddie) (Summers and Felton 1994). Our chemical analysis showed that the concentrations of both chemicals differed among genotypes, and might be affected by N levels and other environmental factors. This suggests a potential relationship between the quantity of these two chemicals and host plant resistance. The lack of a clear relationship of these chemicals with sweetpotato weevil resistance shown in this study is possibly due to the feeding behavior of the weevil in which the beetles chew through the periderm and feed on the tissue beneath it. It is also possible that the sweetpotato weevil can metabolize or sequester these harmful chemicals.

In summary, nitrogenous fertilizer had a slight effect on sweetpotato weevil oviposition under both no-choice and choice testing conditions, but not on their feeding activities. Sweetpotato weevil oviposition is an important criterion used to compare the resistance levels of genotypes. The level of N during the growing season should be uniform so as to avoid any bias on the outcome of resistance bioassays. In addition, 'year' appears to have an effect on sweetpotato weevil feeding, oviposition, and plant chemistry. Therefore, sweet potato germplasm should be screened over multiple years before drawing conclusions about the presence or absence of resistance. Sweetpotato weevil resistance did not have a clear relationship with the concentrations of resin glycosides and caffeic acid in the root periderm of the resistant genotypes evaluated in this study.

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